KRILL-FEEDING BEHAVIOUR IN A CHINSTRAP PENGUIN *PYGOSCELIS ANTARCTICA* COMPARED WITH FISH-EATING IN MAGELLANIC PENGUINS *SPHENISCUS MAGELLANICUS*: A PILOT STUDY

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SUMMARY

TAKAHASHI, A., DUNN, M.J., TRATHAN, P.N., CROXALL, J.P., WILSON, R.P., SATO, K. & NAITO, Y. 2004. Krill-feeding behaviour in a Chinstrap Penguin *Pygoscelis antarctica* compared with fish-eating in Magellanic Penguins *Spheniscus magellanicus*: a pilot study. *Marine Ornithology* 32: 47-54.

Inferring feeding activities from undulations in diving depth profiles is widespread in studies of foraging marine predators. This idea, however, has rarely been tested because of practical difficulties in obtaining an independent estimate of feeding activities at a time scale corresponding to depth changes within a dive. In this study we attempted to relate depth profile undulations and feeding activities during diving in a single Chinstrap Penguin *Pygoscelis antarctica,* by simultaneously using a conventional time-depth recorder and a recently developed beak-angle sensor. Although failure in device attachments meant that data were obtained successfully from just a part of a single foraging trip, our preliminary results show a linear relationship between the number of depth wiggles and the number of underwater beak-opening events during a dive, suggesting that the relative feeding intensity of each dive could be represented by depth-profile data. Underwater beak-opening patterns of this krill-feeding penguin species are compared with recent data from three fish- and squid-feeding Magellanic Penguins *Spheniscus magellanicus.*

Key words: Chinstrap Penguin, Magellanic Penguin, *Pygoscelis antarctica, Spheniscus magellanicus,* Antarctica, Argentina, diving behaviour, foraging ecology

INTRODUCTION

Penguins are important avian consumers of crustaceans and fish in the Southern Ocean (Woehler 1995), and their diving behaviour has been studied extensively over the last decade, thanks to technological advances in time–depth recorders (for reviews, see Wilson 1995, Kooyman 2002). One of the common assumptions in these studies is that undulations in dive profiles indicate feeding activity (Kirkwood & Robertson 1997, Luna–Jorquera & Culik 1999, Hull 2000, Rodary *et al.* 2000, Tremblay & Cherel 2000). However, this assumption has rarely been tested, due to the practical difficulties of obtaining an independent estimate of feeding activity at a time scale corresponding to depth changes within a dive (but see Ropert–Coudert *et al.* 2001, Simeone & Wilson 2003).

The recent development of beak-angle loggers (inter-mandibular angle sensor: Wilson *et al.* 2002) has provided a unique opportunity to examine the beak-opening activity of free-ranging penguins. In conjunction with depth records, data on beak-opening events are capable of indicating feeding (when penguins are underwater) and breathing (when penguins are at the surface) in relation to diving behaviour (Wilson *et al.* 2002, Wilson *et al.* 2003). This technology has previously been applied to free-ranging Magellanic Penguins *Spheniscus magellanicus* (Wilson 2003, Simeone & Wilson 2003), a fish- and/or squid-feeding species (Williams 1995), although not yet to any penguin species that feeds mainly on krill.

Chinstrap Penguins *Pygoscelis antarctica* feed almost exclusively on krill in inshore areas of the Antarctic Peninsula and Scotia Sea region during their breeding season (Lishman 1985, Trivelpiece *et al.* 1990, Lynnes *et al.* 2002, Takahashi *et al.* 2003a). Here, we present an analysis of the beak-opening activities of a single free-living Chinstrap Penguin in relation to diving behaviour, by using a beak-angle logger. We also compare the results with similar data obtained from three free-living Magellanic Penguins feeding on fish (Wilson 2003). The Magellanic Penguin data have been presented elsewhere (Wilson 2003), but we use them in a new context in this paper. We (1) describe the patterns of beak-opening in both penguin species, (2) examine the utility of dive-profile data for indicating feeding activities in Chinstrap Penguins, and (3) discuss differences of feeding patterns between Chinstrap (krill-feeding) and Magellanic (fish- and squid-feeding) Penguins.

METHODS

Chinstrap Penguins

Breeding Chinstrap Penguins were studied during January through early February 2003 (guard to early crèche phases) at Signy Island (60°72′S, 45°36′W), South Orkney Islands, Antarctica. Eight birds

were equipped with loggers measuring depth and beak-angle, although only one bird provided reliable data (see Results). Diving depth was measured every second (with an accuracy of 1 m and a resolution 0.05 m) with time–depth recorders (UME-DT, a cylindrical container with a domed leading end: diameter, 15 mm; length, 50 mm; mass, 14 g; Little Leonardo, Tokyo, Japan). Another logger type, an inter-mandibular angle sensor (IMASEN), consisted of a Hall sensor (diameter: 2 × 3 mm) linked via a thin cable to a logger (75 × 33 × 22 mm; mass, 42 g; Driesen & Kern, Bad Bramsted, Germany—for details, see Wilson *et al.* 2002, Wilson 2003). The sensor, which was fixed to the upper beak using a drop of two-component epoxy (RS Components, Corby, UK) sensed magnetic-field strength from a small neodinium boron rare-earth magnet (8 × 8 × 6 mm) attached similarly to the lower beak. Strength of the magnetic field registered by the sensor varied with beak angle. The relationship between output from the Hall sensor and beak angle was ascertained by allowing the birds to bite onto rods of known diameter while the position within the beak at which the rod was bitten, as well as beak and head measurements, was noted. Simple trigonometry allowed calculation of the beak angle. Data were recorded at 10 Hz. Time–depth recorders and beak-angle loggers were attached to the lower backs of the birds to minimise drag (Bannasch *et al.* 1994), using Tesa tape (Wilson *et al.* 1997). The cable of the beak-angle logger was placed over the bird's head and directly down the bird's back to the logger, being held in place by spots of glue at intervals. The attachment took about an hour and depended mainly upon the time required for the glue to set.

Magellanic Penguins

The study was conducted during November and December 2000 when three Magellanic Penguins, brooding chicks in the Cabo Virgenes colony (52°24′S, 68°26′W), Santa Cruz, Argentina, were equipped with IMASENs in a manner similar to that described above for Chinstrap Penguins. Minor differences were that Poxypol was used as a two-component glue to attach the sensors and magnets to the birds, and that the time taken to equip the birds was less than 35 minutes, principally because the glue set more rapidly. In addition, leg-fitted (see Simeone *et al.* 2002) time–depth recorders were used (Lotek, St Johns, Newfoundland, Canada; diameter, 57 × 18 mm; mass, 16 g), set to record depth data at 1 Hz (for further details, see Wilson 2003). Birds were left to forage for a single trip before the devices were recovered.

Data analyses

Diving depth and beak-angle data obtained from the loggers were analysed for Chinstrap Penguins with custom-designed macro-programs in Igor Pro (Wave Metrics, Inc., Oregon, USA) or for Magellanic Penguins with the software MT-beak supplied by Jensen Software Systems (Laboe, Germany). Because the pressure sensor of time–depth recorders sometimes shows a drift associated with ambient temperature (±0.5 m at the maximum), we obtained surface pressure by assuming the birds would be at the surface at least once within a 300-s period (this being more than the maximum dive duration recorded for Chinstrap Penguins: Takahashi *et al.* 2003a) and took the minimum pressure reading within the 300-s period as the surface pressure. After these 0-m calibrations, a dive was considered to occur if maximum depth exceeded 1 m (Takahashi *et al.* 2003a). The programs calculated maximum dive depth, dive duration, surface interval, bottom time (the time between the start and end of the time when birds showed depth change of 0 m) and the number of depth wiggles for each dive. A "depth wiggle" was defined as the event when birds changed their swim direction from descending to ascending. In the Chinstrap Penguin, the baseline of beak-angle data (i.e. the beak-angle readings without conspicuous beak-opening) drifted gradually (up to +2.0º), possibly because the magnet on the beak gradually became loose due to use of non-optimal glue or because electronic drift occurred in the sensor. To obtain the correct baseline, the same approach to 0-m calibration of depth data was undertaken. We obtained the baseline by assuming that a beak-opening event should last less than 8 s (based on the maximum duration of beak-opening events recorded for Magellanic Penguins: Wilson 2003) and considered the minimum beak-angle reading within the 8-s period as the baseline of beak-angle data. Because the maximum beak-angle for particular activities was similar before and during the baseline drift (for example, the beak-angle for breathing, A. Takahashi *et al.* unpubl. data), we are confident that the drift was corrected successfully. A beak-opening event was considered to occur if the penguin beak-angle exceeded 2.0º from the baseline, following Wilson (2003). Our program calculated the maximum beak-angle and the duration for each beak-opening event. The depth at each beak-opening event was defined as the nearest depth record.

RESULTS

All three of the Magellanic Penguins equipped returned to their nests after having been at sea for a maximum period of 21.6 h. All had fed successfully (as judged by their protruding bellies, by their provisioning of their chicks and by inspection of the IMASEN data—for more detail, see Wilson 2003). However, of the eight Chinstrap Penguins equipped, two birds did not return to the colony during the study period. These two birds might have been more sensitive to device effects than other birds since these birds were studied later during the chick-rearing period (see Watanuki *et al.* 1992). One bird returned to the colony after six days, with the magnet and Hall sensor of the beak-angle logger detached. The other five birds returned to the colony with the Hall sensor still attached to the beak, but with the magnet on the beak detached (three birds) or with the cable between the Hall sensor and the logger damaged (two birds). Mean foraging trip duration for these five birds was 17.0±5.8 h, which was similar to that of the birds carrying only time–depth recorders (18.2 h: A. Takahashi *et al.* unpubl. data). On one occasion, the beak-angle logger had no data due to unit malfunction. Of the other birds, the data output from three birds remained near the point of minimum magnetic reading while at sea, indicating that the cable was damaged before the birds went to sea (two birds) or the magnet attached to the beak fell off just after the start of diving (one bird). Consequently, only one bird provided reliable beak-angle data, for a 7.8-h period of its 21-h long foraging trip, until the magnet attached to the bird fell off at sea. Subsequent analyses were carried out using the 7.8-h period of this individual bird.

Dive-depth profiles and beak-angle data indicated two apparent types of beak-opening activities: beak-opening activity underwater and at the surface between dives (Fig. 1). Presumably the former relates to feeding activity and the latter to breathing activity (see Wilson *et al.* 2002, Wilson *et al.* 2003, Wilson 2003). We confined our analyses to the underwater beak-opening events to focus on feeding activities.

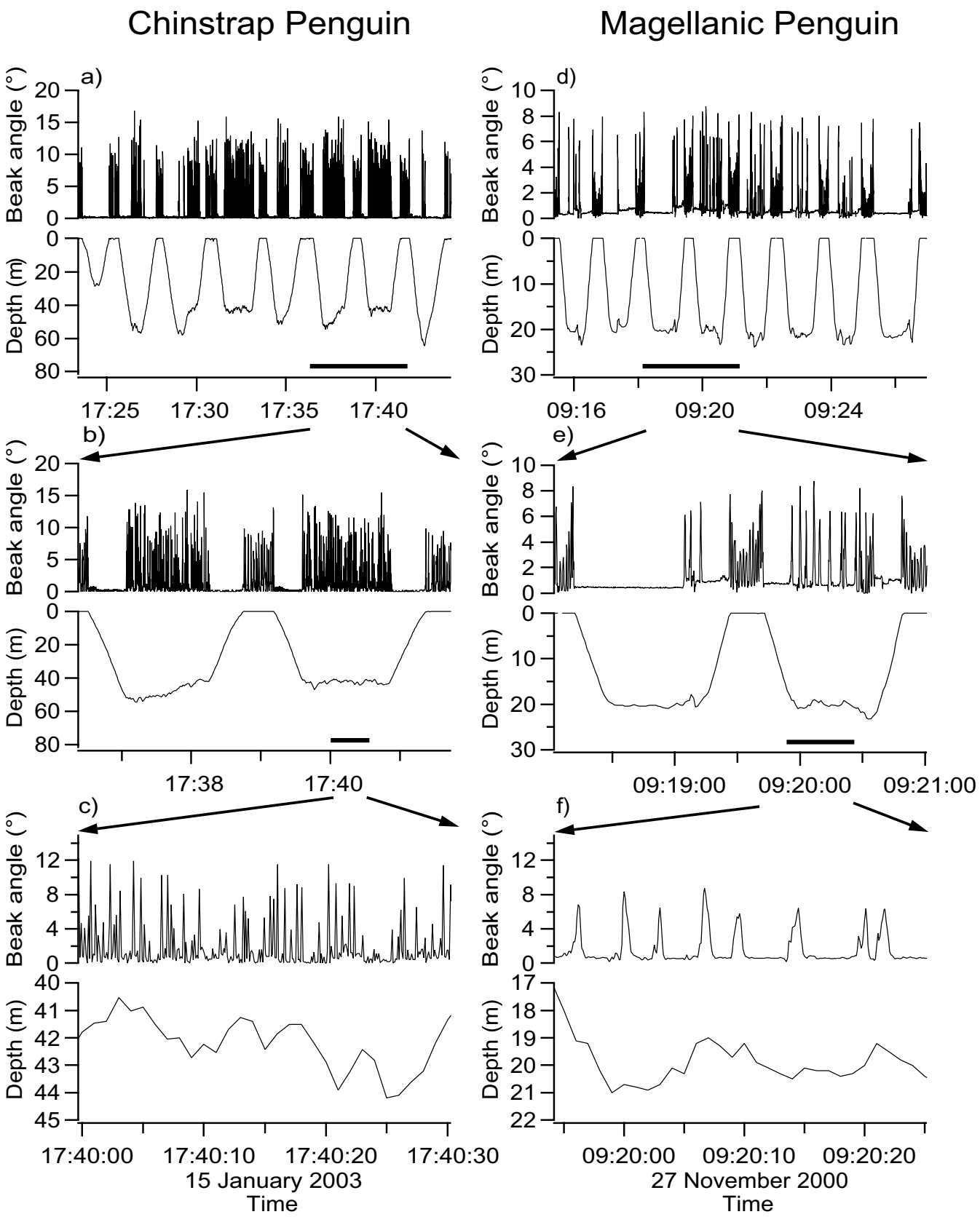


Fig. 1. Relationship between beak-angle over time and dive depth for a Chinstrap Penguin (a,b,c) and a Magellanic Penguin (d,e,f). (a,d) Records over eight dives. (b,e) Enlarged records for two dives. (c,f) Thirty seconds during the bottom phase of a dive when many prey were captured.

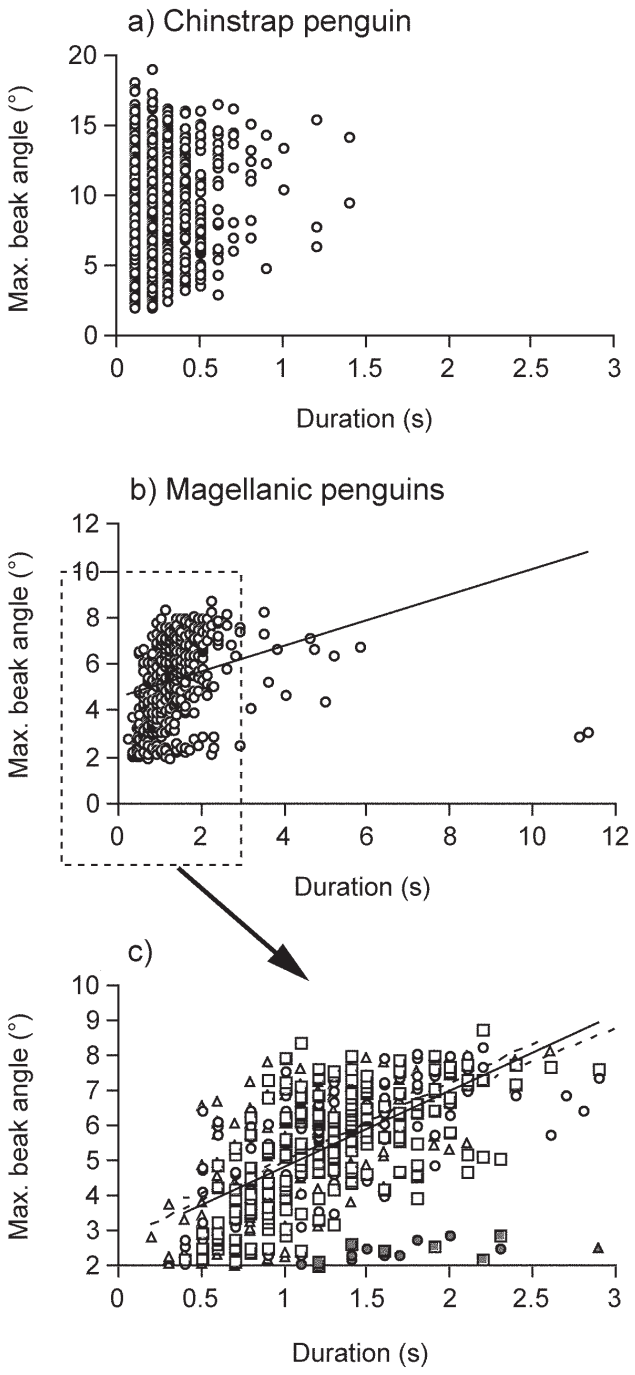


Fig. 2. Relationship between maximum beak-angle per beak-opening event and duration of the beak-opening event for (a) a Chinstrap Penguin feeding on krill and (b,c) three Magellanic Penguins feeding on fish. The regression equation combined for three Magellanic Penguins (b) is Y = 0.55X + 4.58 (n = 600 beak-opening events, r^2 = 0.08). Because the data show outliers, we derived an index dividing the maximum beak angle by the duration. All data with an index of less than 2.0 (31 data points) were excluded when calculating the regression equation for each of the three Magellanic Penguins (c: different symbols for each bird). Regression equations are Y = 2.19X + 2.56 (r^2 = 0.41), Y = 1.86X + 3.18 (r^2 = 0.42) and Y = 2.24X + 2.74 (r^2 = 0.41), where the outliers (shaded symbols) are excluded.

Underwater beak-opening events in the single Chinstrap Penguin study bird were of very short duration (mean duration, 0.13 s; maximum duration, 1.4 s; 82% of the events lasted ≤0.1 s; n = 4910) with angles up to 19.0º [Fig. 2(a)]. In the Magellanic Penguins, the beak-opening events were longer (ANOVA, F = 8606.0, P < 0.0001; mean duration, 1.3 s; maximum duration, 11.3 s; 82% of the events lasted <1.7 s; n = 600) with angles up to 8.7º [Fig. 2(b,c)]. There was no relationship between the maximum beak-angle and beak-opening duration for beak-opening events in the Chinstrap Penguin, although there was a positive relationship for all three Magellanic Penguins (Fig. 2).

Dive-depth profiles and beak-angle data showed variation in the number of underwater beak-opening events between dives for both penguin species [Fig. 1(a,d)]. Indeed, the number of beak-opening events per dive varied considerably, although the variation was higher in the dives made by the Chinstrap Penguin (mean, 52.8±40.3; range, 2–150 events per dive, for n = 93 successful dives) than in any of the Magellanic Penguins (means, 3.8±3.1, 5.9±4.0 and 11.0±3.7, for a total of 600 successful dives by three Magellanic Penguins). We do not consider that it is appropriate to present mean number of events per dive regardless of whether the dive was successful, because penguins perform many dives to travel rather than to forage and this needs further careful consideration.

The following results are presented only for the Chinstrap Penguin, given that these types of data have already been presented for the Magellanic Penguins elsewhere (Wilson 2003, Simeone & Wilson 2003). Underwater beak-opening events occurred rarely (1 out of 181) in shallow dives [<5 m, Fig. 3(a,b)]. The number of underwater beak-opening events per dive increased for dives with a maximum dive depth deeper than 30 m [Fig. (3b)]. For deeper dives (>5 m), the number of depth wiggles showed a significant positive linear relationship with the number of underwater beak-opening events during dives (Fig. 4). Dive bottom duration also showed a significant positive linear relationship with number of underwater beak-opening events during dives (regression equation: No. beak-opening events = 1.5 × Bottom duration(s) – 2.6; n = 117 dives, r^2 = 0.71, P < 0.0001), although the coefficient of determination (r^2) of the regression was lower than that for the number of depth wiggles.

Beak-opening events occurred mostly during the bottom periods of the dives (86%: 4241 of 4910 events recorded), rather than during descending (2%: 85 events) or ascending (12%: 584 events) periods. During the bottom periods of the dives, beak-opening events occurred more often when the Chinstrap Penguin was ascending than when it was descending [Fig. 5(a,b); chi-square test for equal probability: χ^2 = 195.1, P < 0.0001].

DISCUSSION

Care is required when considering foraging behaviour from device-derived data, because device attachment itself is known to affect many aspects of swimming and diving behaviour (e.g. Wilson *et al.* 1986). All three Magellanic Penguins appeared to have foraged normally, although there has been some discussion of the effects of IMASENs on penguins in Wilson *et al.* (2002) and Wilson (2003). The single individual Chinstrap Penguin analysed here had a foraging trip duration (21 h) and diving depth (maximum dive depth 82 m) comparable to previous records for Chinstrap Penguins from Signy Island (19.9 h for average overnight trip duration and

modal maximum dive depth 80–100 m; Takahashi *et al.* 2003a) and clearly fed extensively while diving to considerable depths. As a result we believe that the effects of the device attachment in this case were not dissimilar to those for other devices (see Takahashi *et al.* 2003a) and that, in general, bird behaviour was not greatly modified. However, three of eight Chinstrap Penguins showed unusually long foraging trips, which suggests that this technology, or the manner in which birds were equipped, needs improvement. Specifically, the time required to attach devices to the beak of the birds was longer in Chinstrap as compared with Magellanic Penguins, and this may have imposed stress on the birds and induced unusually long foraging trips for some. In addition, the failure of magnet attachments indicates that more research is needed into appropriate quick-setting glue (which may also help reduce handling stress to the birds). Minimization of damage to the cable connecting the Hall sensor and the logger also needs research. With regard to the latter, if the cable were to be covered by feathers, damage due to pecking during preening may be reduced because the cable may be less conspicuous to the birds.

Another issue that needs care in our results would be lack of information about potential inter-individual variability for the case of the Chinstrap Penguin. Although the three Magellanic Penguins used for this study showed relatively consistent characteristics in

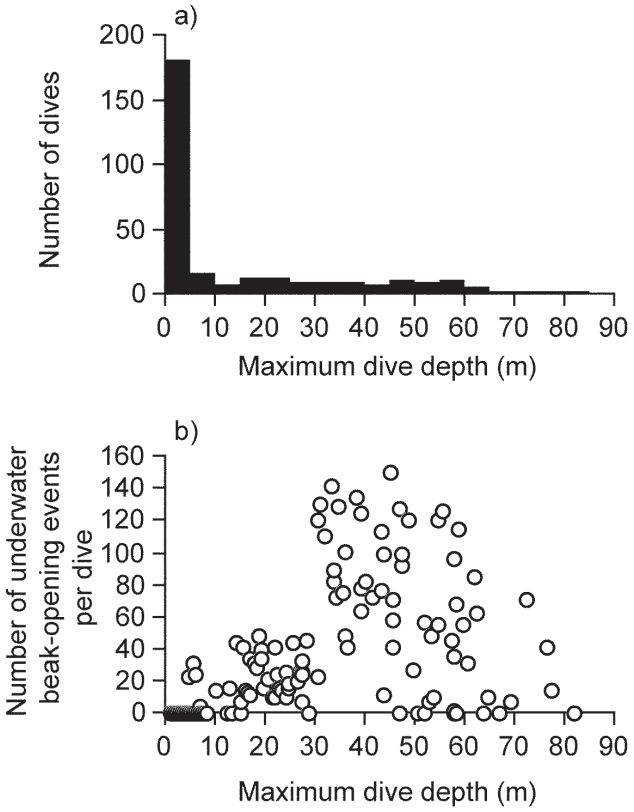


Fig. 3. (a) Frequency distribution of maximum dive depth. (b) Relationship between maximum depth of dive and number of underwater beak-opening events per dive in a Chinstrap Penguin.

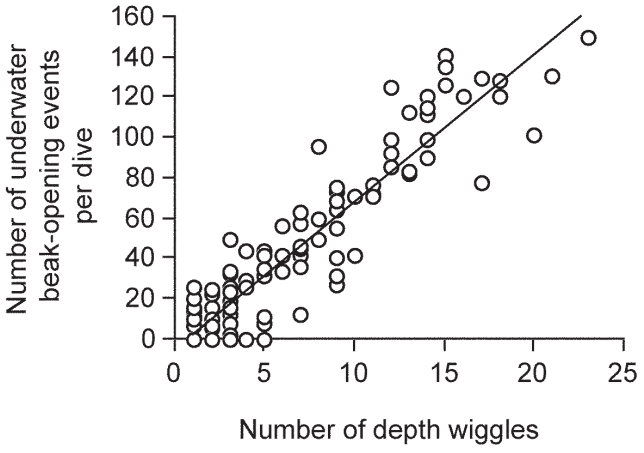
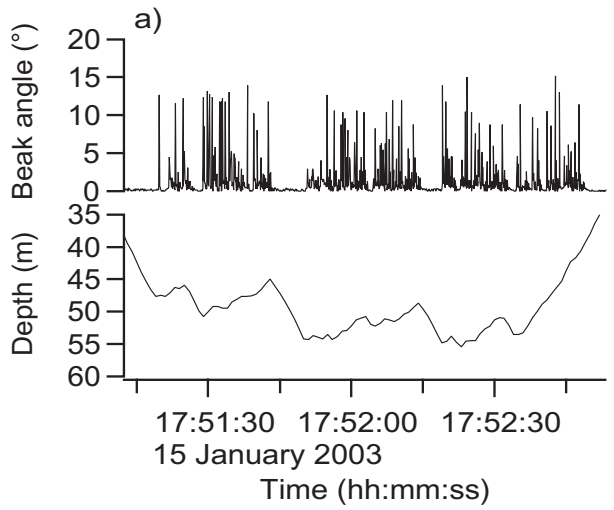


Fig. 4. Relationship between number of depth wiggles and underwater beak-opening events per dive (>5 m) in a Chinstrap Penguin. Regression equation is Y = 7.3X – 5.3 (n = 117 dives, r^2 = 0.85, $P < 0.0001$).



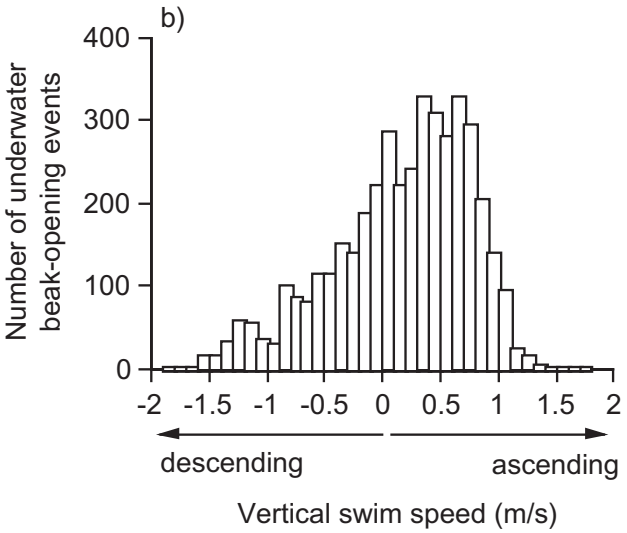


Fig. 5. (a) A selected depth and beak-angle record for a Chinstrap Penguin showing frequent feeding during short ascent periods at the bottom phase of a dive. (b) Number of underwater beak-opening events in relation to vertical swim speed during the dive bottom period of a Chinstrap Penguin. Note that beak-opening events occurred more often when birds were ascending than when they were descending.

their beak-opening patterns [Fig. 2(c)], large inter-individual variation in diving parameters has been reported in some penguin species (Wilson *et al.* 1996, Takahashi *et al.* 2003b), which necessitates interpreting our results with caution.

Relationship between undulations in depth and prey capture

Although our study on the Chinstrap Penguin is based on a single bird for a period of 7.8 h, one of the important findings is the correspondence between depth wiggles and underwater beak-opening (Fig. 4). The linear relationship between the number of depth wiggles and the number of underwater beak-opening events suggests that the number of depth wiggles per dive could be a good indicator of relative feeding intensity. This has already been shown for fish-eating Magellanic Penguins (Simeone & Wilson 2003). However, given that Chinstrap Penguins breeding at Signy Island feed almost exclusively on swarming crustaceans (99.8%–100% by mass; Lynnes *et al.* 2002, Takahashi *et al.* 2003a), this supports the possibility of a general case for undulations in the depth profile being associated with prey capture in marine endotherms. This assumes that beak-opening underwater is associated with prey ingestion, which has been shown to be the case at least in captive penguins (see discussion in Wilson *et al.* 2002). Simeone & Wilson (2003) and Wilson (2003) note that prey ingestion in penguins is invariably associated with a right-hand skew in the graph of beak-angle over time and suggested that this is due to the process of the prey passing the mouth during the final stages of ingestion. Such a right-hand skew was indeed observed on all occasions when the equipped Magellanic Penguins opened their beaks underwater, apart from single opening events immediately after the head was immersed (Ropert–Coudert *et al.* 2002). It would seem, therefore, that the hydrodynamic disadvantages incurred by opening the beak underwater at speed tend to lead to penguins opening their beaks only when prey capture is assured. Our IMASEN measurement interval of 10 Hz was not rapid enough for us to be able to ascertain whether beak-openings in the Chinstrap Penguin had a right-hand skew, given that the majority of opening events lasted about 0.1 s [Fig. 2(a)]. We therefore cannot be sure that each beak-opening was associated with prey capture. However, given that Magellanic Penguins essentially open their beak underwater only to feed, we believe that the Chinstrap Penguin studied did the same.

The Chinstrap Penguin appeared to feed more often during short ascent periods in the bottom phases of the dives [Fig. 5(a,b)]. Prey ingestion associated with an upward swim direction has also been reported in the congeneric Adélie Penguin *P. adeliae,* using data from oesophageal temperature loggers (Ropert–Coudert *et al.* 2001). These authors hypothesized that birds may use backlighting to detect and capture their prey and that this may allow a predator to be better camouflaged itself by not being backlighted. Another not mutually exclusive hypothesis would be that birds may approach prey from underneath and thus remain more difficult to detect by the prey, given that euphausiid crustaceans may be less capable of seeing beneath them due to the position of their eyes, which are situated just above their large feeding appendages (Mauchline & Fisher 1969).

Inter-specific comparison of the prey ingestion characteristics from the IMASEN

The two species used in this study take very different types of prey, with Magellanic Penguins feeding primarily on fish (mainly *Sprattus fuegensis* and *Odontesthes smitti*) a few centimetres long, weighing between about 4 g and 30 g (Scolaro *et al.* 1999), and with Chinstrap Penguins feeding on Antarctic Krill *Euphausia superba* weighing about 1 g (Hofmann & Lascara 2000, Lynnes *et al.* 2002, Takahashi *et al.* 2003a). Given the differences in size and behaviour of these two prey types, we would expect major differences in the rates at which they are acquired, as well as differences in the pattern and characteristics of beak-opening events associated with prey capture. Most of the (very few) direct observations (e.g. by Sir Douglas Mawson at Falla (1937) for Adélie Penguins) and the numerous inferential assessments (Zusi 1975) suggest that all penguins take prey individually. Thus, although our sample sizes are small, major differences were apparent in both the frequency of beak-opening events and in beak-angles. The number of prey items caught during successful dives by the Chinstrap Penguin studied was 53 prey items on average—which is about 53 g, assuming an average individual prey mass of 1 g. This contrasts with the Magellanic Penguins, which caught an average of 4–11 prey items per dive, or 16–44 g per dive, assuming a mean individual prey mass of 4 g for the Cabo Virgenes region (Scolaro *et al.* 1999, J.A. Scolaro *et al.* unpubl. data). A more detailed analysis of dive types, together with larger sample sizes is now needed to give such figures a wider context.

Wilson *et al.* (2002) suggested that the integral of beak-angle over time could be used as an index of prey mass. Our results indicate that Magellanic Penguins show a relationship between maximum beak-angle and duration during ingestion, even though there are clear indications that certain individual prey fall away from the regression line, perhaps due to prey-handling difficulties and/or to differently-shaped prey [Fig. 2(b,c)]. This was not the case for the Chinstrap Penguin, which appeared to catch very small prey with a variable 'snap'. It is doubtful whether the relationship between integral and prey mass would hold for penguins feeding on prey as small as krill. Ultimately, this question cannot be resolved by our data from the Chinstrap Penguin because the sampling rate of 10 Hz does not provide the resolution necessary to describe the form of the prey-ingestion peaks over time [Fig. 2(a); see Ropert–Coudert & Wilson (2004) for a discussion of this]. Further research is therefore needed on a greater number of birds equipped with IMASENs that have a higher recording frequency. Studies on captive birds would also provide useful information on the mechanism by which krill-eating penguins capture prey. For example, more than one prey is ingested at the same time, and this may account for the unusually high beak-angles at times. This might be possible given the high densities of krill swarms (Hamner & Hamner 2000).

Our study indicated that the use of beak-angle measurement has considerable potential for inferring, and potentially quantifying, key aspects of the foraging behaviour of penguins. However, further studies, particularly of species with contrasting prey and feeding ecology, are needed to develop these initial results.

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